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A squeeze in the suitable fire interval: Simulating the persistence of fire-killed plants in a Mediterranean-type ecosystem under drier conditions

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ABSTRACT

Mediterranean-type ecosystems (MTEs) harbor an exceptionally high biodiversity of vascular plants. At the same time, climatic conditions in many MTE regions are projected to become both drier and hotter, and fire intervals shorter. The Interval Squeeze conceptual model integrates the potential effects of a changing climate and fire regimes on perennial plant population persistence and postulates that warmer, drier conditions will negatively affect multiple plant demographic processes. Dependent on species-specific traits, the required fire intervals that allow for population persistence might become longer, while projected future fire intervals are shorter, leading to a potential mismatch. However, conceptual models are per se not able to quantify outcomes of multiple stochastic processes or to simulate temporal dynamics. Here, we develop a simple, process-based model for a fire-sensitive woody plant species to evaluate the response of demographic processes to future climatic conditions and to quantify the potential impact also of future changes in fire interval. This allowed us to assess key assumptions of the interval squeeze model, particularly in relation to demographic drivers.

We simulated populations of *Banksia hookeriana*, a typical fire-killed shrub found in MTEs of South-West Australia which stores its seeds in a canopy (serotinous) seedbank and shows strong cohort recruitment in the first year after fire. We estimated suitable fixed fire intervals for population persistence under historic climatic conditions and evaluated impacts of a higher dry year frequency (as projected under future climate by two representative concentration pathways, RCP4.5 and RCP8.5). Our findings support the Interval Squeeze Model: the fire interval allowing plant population persistence is squeezed from currently 10–28 years to 13–28 years for RCP4.5. For RCP8.5 population persistence is not possible under any of the tested fire intervals because of low seed production and low survival probability of both seedlings and adult plants. The results show that projected drier conditions alone will cause a higher extinction risk for fire-sensitive perennial plant populations in MTEs, which is further pronounced in combination with shorter fire intervals. This will likely lead to a strong shift in community composition and a loss of biodiversity. Fire management practices may need to be modified to attempt to counteract prospective biodiversity loss and ecosystem structure change.

1. Introduction

Mediterranean-type ecosystems (MTEs) cover only slightly more than 2% of global land area but support 20% of the world's plant species (Hobbs et al., 1995). Evergreen and sclerophyllous shrubs and trees dominate these areas, with most plants being endemic (Specht and Moll, 1983). These ecosystems are characterized by a climate regime with mild, wet winters and warm, dry summers, nutrient-poor soils, and regular disturbance by fire. Fire partly compensates for nutrient limitation through the episodic input of nutrient-rich ash (Groom and Lamont, 2015). Due to their high level of biodiversity and endemism, MTEs are highly vulnerable to species losses as a result of climate change (Thomas et al., 2004). Climate projections suggest that climate will become both warmer and drier, leading to reduced water availability (Diffenbaugh and Field, 2013). In addition, fire intervals will shorten in many regions, because weather conditions conducive to fire may occur more frequently (Moritz et al., 2012a,b). MTE plant populations are adapted to regular fire, for example through the ability to resprout from protected tissues or through regeneration from soil-, or canopy seed banks. Although the vegetation in MTEs is adapted to dry conditions and frequent fires, climate change is expected to negatively affect plant populations and to lead to major changes in these plant communities (Esther et al., 2010; Mouillot et al., 2002).

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More frequent fire and reduced water availability produce multiple stressors, which affect vegetation in MTEs simultaneously. Multiple stressors have gained attention in global change research because their effects can be synergistic, i.e. their joint effect can be larger than the sum of the single effects (Crain et al., 2008). Therefore, they potentially undermine the limited resilience of ecosystems. The synergistic effects of climate change affect various demographic processes of MTE vegetation simultaneously. Higher fire frequencies in combination with a higher likelihood of dry years increase the probability that a fire is followed by unfavorable weather conditions leading to high seedling mortalities of species that use fire cues to germinate (Enright et al., 2015). When demographic rates (i.e. growth and reproduction) are slowed down due to unfavorable climate conditions (Pereira et al., 2007) or when the subsequent fire follows too soon, the risk increases that plants will lack a sufficient seedbank for self-replacement (Westerling et al., 2011). The existence of multiple stressors impedes the assessment of climate change effects on ecosystems because i) stressors may affect different processes within the ecosystem ii) quantifying synergistic effects such as the examples described above requires understanding their joint impacts.

To elucidate the effects of climate change on woody plants in fire driven ecosystems Enright et al. (2015) proposed the conceptual Interval Squeeze Model. This model comprises three essential shifts that could potentially mediate the impact of a drying and warming climate on plant populations: i) demographic shift, characterized by a prolonged juvenile stage and reduced seed production ii) post-fire recruitment shift, i.e. decreased recruitment of seedlings due to a higher likelihood of adverse weather conditions in the first few years after fire, and iii) fire-interval shift, which describes shortened fire-intervals under drier and warmer conditions. They concluded that under future conditions, the required fire interval for population survival might become longer, while the actual fire interval will become shorter, leading to a squeeze of the survival window (interval squeeze) and thus a potential threat to population persistence.

The model of Enright et al. (2015) is – like other conceptual models – a highly useful tool to generate hypotheses on the relevance of different drivers in complex situations such as climate change effects on ecosystems. To some degree, the conceptual model can be tested by empirical data on different processes (e.g. determining seed production, germination rates or seedling survival dependent on weather conditions), however, it may be more difficult to disentangle e.g. different demographic effects on population survival and to make long-term assessments of population viability. Building on the ideas of the Interval Squeeze Model, Batllori et al. (2017) developed a cellular automaton model to study the cumulative effects of altered fire frequencies and droughts on forest and shrubland vegetation in MTEs. To test for synergistic effects, they defined individual-, and compound drought and fire scenarios but did not find long-term synergistic effects of fire and drought on the composition of broad vegetation types at the landscape level. However, since their cellular automaton model did not account for drought effects on specific demographic processes, it could not fully test the Interval Squeeze Model and the contribution of single demographic processes to population viability. To our knowledge, no systematic assessment of the effects of changing demographic rates exists so far, therefore a quantitative testing of the Interval Squeeze Model and its effect on long-term population survival is still incomplete.

In this study, we present a process-based model describing the fate of individual plants belonging to a local plant population of the species *Banksia hookeriana* to test key aspects of the Interval Squeeze Model. We chose *B. hookeriana* as a typical serotinous, non-sprouting species, i.e. a species that is killed by fire and recruits from a canopy seedbank. The model is parameterized based on empirical data from the fire-prone South-West Australian botanical province and assesses the viability of the population by simulating demographic processes dependent on fire and weather conditions. We use the simulation model to evaluate the contribution of the three potential shifts (demographic, post-fire recruitment and fire-interval shift) on population variability and the squeeze of the survival interval in response to drier conditions under two representative future climate scenarios (RCP4.5 and RCP8.5, Vuuren et al. (2011)).

2. Methods

2.1. Study site

Demographic data on *B. hookeriana* and on climate conditions are based on empirical data from the Eneabba sandplain, South-West Australia, about 270 km north of Perth. The long-term average annual rainfall in this area is ~500 mm/year with rain predominantly falling in winter between May and August. Maximum summer temperature between December and March is frequently above 40 °C (Bureau of Meteorology, 2017). The soil consists of nutrient poor sands overlaying clay or laterite, and low sandy dunes to 10 m local relief determine the topography (Cowling et al., 1996; Hnatiuk and Hopkins, 1980). The vegetation mainly consists of dense sclerophyll shrubland. The flora is species-rich and dominated by Proteaceae, Myrtaceae, Epacridaceae and Restionaceae (Groom and Lamont, 2015).

2.2. Studied species

We use demographic data for *B. hookeriana* (Proteaceae). The species` range is comparatively small (< 5000 km^2, Miller et al., 2007) and restricted to the northern sandplains of South-West Australia. *B. hookeriana* is a fire killed and highly serotinous shrub (Enright et al., 1996). Thus, it represents a plant strategy that is very common in sclerophyllous shrublands in MTEs (Cowling et al., 1996; Pausas et al., 2004), but potentially disadvantageous under climate change (Enright et al., 2015). In addition, the demography of *B. hookeriana* has been extensively explored in the field and in modelling studies (Enright et al., 1998, 1996; Groeneveld et al., 2008, 2002; Keith et al., 2014; Lamont et al., 1989).

2.3. Model description

In the following, we briefly describe the simulation model. A full model description following the ODD protocol ('Overview, Design concepts, and Details', Grimm et al., 2006, Grimm et al., 2010) as well as a link to the model code is given in the supplementary material (Appendix A). The model simulates the fate of a local population of *B. hookeriana*. While seeds in each cohort and seedlings are represented by their total number, the demography (seed production and storage, survival) of mature plants is simulated for each individual. Our model runs on an annual temporal resolution and is not spatially explicit but implicitly covers an area of 100 m by 100 m. Under the assumption that a mature plant needs a minimum area of 2 m by 2 m (Esther et al., 2008), the maximum population size is 2500 plants.

2.3.1. Process overview

The model calculates the fate of individual plants dependent on yearly weather conditions (average versus dry) and fire occurrence (Fig. 1, for details see Section 2.4 and ODD-Protocol in Appendix A). In each year without fire, mature plants produce seeds, which are stored in the canopy. The annual survival probability of seedlings and mature plants is age- and weather-dependent. After a certain, weather-dependent number of years seedlings become mature plants. In years with fire, mature plants disperse their seeds and all plants die. Triggered by the fire event, all seeds germinate in the next winter, leading to an even-aged plant cohort. All parameter values of the modelled processes are given in Table 1.

All processes were implemented in NetLogo Version 6.0.2 (Wilensky, 1999) and results were analyzed with R Version 3.4.3 (R Core Team, 2017).

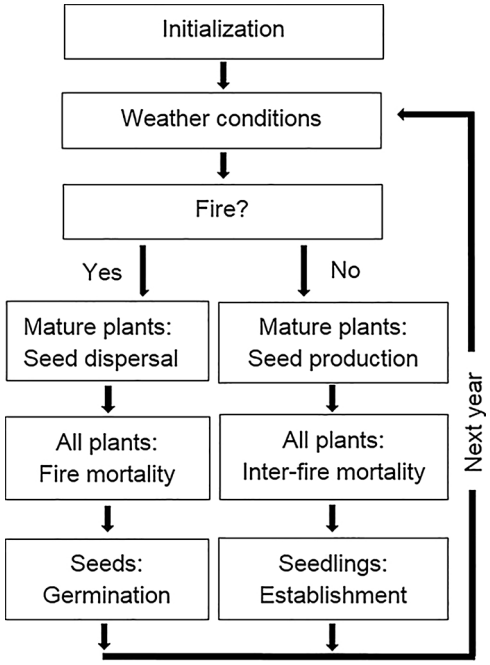

Fig. 1. Overview of simulated processes in the population model of B. hookeriana. All processes are simulated spatially implicitly.

2.3.1.1. Initialization. The model is initialized with a starting population of 2500 5-year old mature plants, for which seed production is just about to start. That is, we assume the last fire event to have occurred five years ago. Weather conditions in the first year are average.

2.3.1.2. Weather conditions. Following the approach by Esther et al. (2008), each year is either classified as average (annual rainfall between 555 mm and 376 mm) or dry (annual rainfall below 376 mm, i.e. more than 20% below average). The simulated climate scenarios, which determine the probability of average and dry years, are described below in Section 2.4).

2.3.1.3. Fire event. To allow for a systematic assessment of altered fire interval effects, we tested fixed, non-random fire intervals. We chose fixed rather than a random return interval to increase the traceability of the results. The estimated mean fire interval for shrublands of the Eneabba Sandplain over the past four decades is 13 years (Miller et al., 2007).

2.3.1.4. Seed dispersal. *B. hookeriana* plants release all seeds after a fire event. Since the model is spatially implicit, these seeds are assumed to be evenly distributed across the modelled landscape.

2.3.1.5. Fire mortality. *B. hookeriana* lacks the ability to re-sprout (Enright and Lamont, 1989), thus the local plant population dies when fire occurs.

2.3.1.6. Germination. The simulated plants require fire to cue germinate. Thus, germination only occurs in the year after fire. All seeds are assumed to germinate (Esther et al., 2008) without any limitation of seedling number.

2.3.1.7. Seed production. The total number of seeds alive (i.e. the canopy seed store) under average conditions is assumed to follow a logistic function of age, following the approach by Groeneveld et al. (2002).

The derivative of this function leads to the number of seeds gained per year and plant (implicitly including newly produced seeds and seed losses via mortality):

$$\Delta \text{seeds} = \begin{cases} \frac{L \cdot e^{-k \cdot age}}{(1 + M \cdot e^{-k \cdot age})^2} \cdot f_{Dry}, & \text{if last years weather conditions were dry} \\ \frac{L \cdot e^{-k \cdot age}}{(1 + M \cdot e^{-k \cdot age})^2}, & \text{else} \end{cases} \quad (1)$$

The parameters L and k describe the steepness of the growth of the canopy seedbank and M describes the size of the canopy seedbank in the equilibrium. In years following a dry year, seed production is assumed to be reduced by f_{Dry} to 50% of normal production (Keith et al., 2014). Seeds remain in the canopy and are stored until seed longevity age S_{max} (15 years) is reached (Enright et al., 1998).

Table 1
Model parameters.

Parameter	Value		Unit	Reference
	average	dry		
Maximum age of mature plants Age_{max}	40	40	Years	Groeneveld et al. (2002)
Age of maturity Age_{mat}	5	5th year dry: 6 6th year dry: 7	Years	Enright et al. (1998)
Mortality of mature plants < 25 $P_{mortality}$	0.023	0.024		Groeneveld et al. (2002), Enright et al. (2015)
Mortality of mature plants > 25 $P_{mortality}$	0.033	0.035		Groeneveld et al. (2002), Enright et al. (2015)
Inter-fire mortality of seedlings until maturity $P_{mortalityseedling}$	1. year: 0.96 2. year: 0.47 3. year: 0.22 4. year: 0.12 5. year: 0.09 6. year: 0.07 7. year: 0.06	0.97 0.69 0.54 0.50 0.49 0.49 0.48		Enright et al. (1998), Groeneveld et al. (2002)
Steepness of seed production function	L: 27,000 k: 0.4	L: 27,000 k: 0.4		Groeneveld et al. (2002), Keith et al. (2014)
Equilibrium size of canopy seedbank M	90	90		Groeneveld et al. (2002), Keith et al. (2014)
Weather impacts on seed production f_{Dry}	1	0.5		Keith et al. (2014)
Seed longevity S_{max}	15	15		Groeneveld et al. (2002), Keith et al. (2014)

2.3.1.8. Inter-fire mortality of mature plants. The mortality of adult plants in years between fires depends on their age and the weather conditions. Until the age of 25 years the mortality is constant. Afterwards, mortality is higher due to senescence, and plants can reach a maximal age of plants of Age_{max} (40 years). For dry years mortality increases by 6% relative to average conditions (Enright et al., 2015).

2.3.1.9. Inter-fire mortality of seedlings. The mortality of seedlings decreases with age. We follow the approach of Groeneveld et al. (2002) who transformed regression curves of field data to survival probabilities. In dry years seedling mortality is higher than in average years.

2.3.1.10. Establishment. Seedlings become mature plants and start producing seeds at the age of five years under average weather conditions. If weather conditions in the year of establishment are dry, maturity for all plants is delayed by one year, and by two years if the subsequent year also exhibits dry weather conditions. At age seven years, surviving plants become reproductive irrespective of weather conditions (Burrows, 2008; Enright et al., 1998). The number of surviving mature plants is limited to a capacity of 2500 due to spatial constraints. If seedling number exceeds this capacity, the excess seedlings are deemed to have died. Mature plants are thereafter followed individually for seed production and survival.

2.4. Climate scenarios

We simplify annual weather conditions as either dry or average. For the baseline scenario, we calculated the probabilities for dry and average years based on long-term rainfall records from the Dongara climate station, which is the closest climate station to the Eneabba field sites with long-term (> 100 years) rainfall records (Bureau of Meteorology, 2017). For future conditions, we used climate projections for two Representative Concentration Pathways (RCPs, (Moss et al., 2010)). We obtained projections for future conditions (Climate Change in Australia, 2017) for an intermediate emissions scenario (RCP4.5), which reaches a radiative forcing value of 4.5 W/m^2 in 2100, and a high emissions scenario (RCP8.5) with radiative forcing of 8.5 W/m^2 in 2100 (Vuuren et al., 2011). From these, we extracted projections of the relative reduction in monthly precipitation. These were used as input data for a rain generator (see Appendix D) to simulate 200 years of precipitation and to derive probabilities for dry and normal years. In our simulations, we did not account for a gradual transition between present and projected future climates, but rather assessed demographic responses to a given scenario with a constant mean in annual precipitation to better assess the direct impact of given climate conditions instead of memory effects. The probability of dry years increases with climate change intensity (see Table 2).

Table 2
Climate-, and fire scenarios: values for dry years are probabilities, while the fire interval refers to years.

Parameter	Value	Reference
Dry-year-probabilities P_{dry}	Baseline scenario: 0.27 RCP4.5-scenario: 0.42 RCP8.5-scenario: 0.69	http://www.climatechangeinaustralia.gov.au/ date of access: 28.11.2017
Fire interval FI	Current conditions: 13 a Simulated range: 6 - 32 a	Enright et al., 1998, Miller et al., 2007

2.5. Simulation experiments

After evaluating population viability for a time period of 200 years with a fixed fire interval of 13 years under each of the three climate scenarios (baseline scenario with current conditions, RCP4.5 and RCP8.5 scenario), we simulate the Interval Squeeze Model. This simulation follows the original concept of Enright et al. (2015) and consists of four consecutive simulation experiments: *Demographic shift, Post-fire-recruitment shift, Demographic Envelope and Interval Squeeze*. For each experiment, the results for RCP4.5 and RCP8.5 are compared to the baseline scenario (current conditions). The first three experiments show demographic processes following a single fire event and thus show the effects of drier conditions. For this, we run the simulation over 58 years and apply a fire in year 8, in which the age of the population is 13 years. Afterwards, no further fire events are applied. Demographic processes are then evaluated for years 8 to 58, i.e. 0–50 years after the fire has occurred. The forth experiment evaluates population viability over 200 years for fixed fire intervals ranging from 6 to 32 years. All experiments were replicated 30 times for each weather and fire condition to account for stochasticity in mortality and the occurrence of dry years.

Demographic shift describes seed accumulation over time following a single fire event. For 50 years after a fire, we record the number of stored seeds per plant. No further fire event occurs.

Post-fire-recruitment shift estimates the number of four year old seedlings present after a single fire event relative to the number of available seeds stored on plants at the time of fire. Differences between climate scenarios are statistically evaluated using the Wilcoxon rank sum test for non-normally distributed data.

Demographic envelope combines the two previous analyses and shows the resulting relative change in population size. The number of mature plants until 50 years after a single fire event is compared to the number of mature plants at the time of fire. Successful self-replacement is indicated when the ratio is equal to or greater than one. No further fire event occurs.

Interval Squeeze assesses the viability of the plant population under the three climate scenarios for different fixed fire intervals, ranging from 6 to 32 years, which corresponds to the time frame in which viable seeds may be available in the canopy. For short intervals, seed production is very low due to the logistic function of seed production, while at longer intervals, maximum seed longevity has been reached. Results show the survival time of the population during a total simulation time of 200 years for a specified fire interval. We measure the duration of successful survival as the last point in time at which the population shows a successful self-replacement as calculated for the demographic envelope. With this measure we capture that a population might not have gone extinct, yet, but will go extinct in the near future.

2.5.1. Climate change impacts on seeds, seedlings and adults

To analyze the impacts of climate change on different demographic stages of the population we compared the relative change in the number of seeds, seedlings and adult plants between baseline and climate change scenarios. For seeds, we evaluated the numbers at the time of fire (year 8). For seedlings, we evaluated the number four years after the fire (year 12), i.e. in the year before seedlings reach maturity, and for adults, we evaluated the number of mature plants 13 years after a fire (year 21), i.e. at the time when the next fire would occur assuming a regular fire interval of 13 years. For each demographic stage (seeds, seedlings, adult plants), we transposed the data relative to the median value of the respective stage for the baseline scenario. This facilitates assessing the impacts of climate change on each demographic stage.

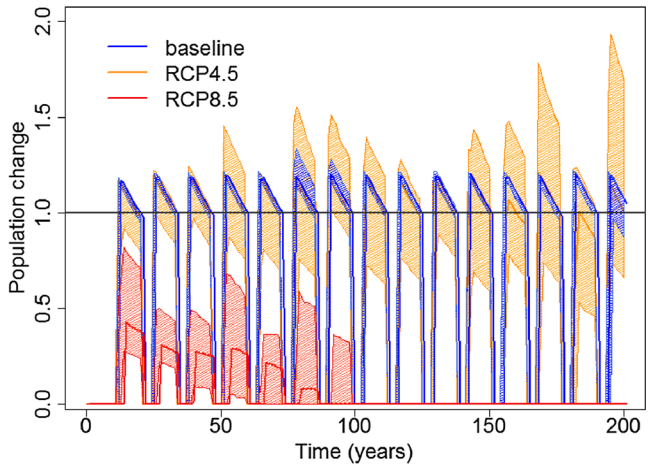

Fig. 2. Demographic envelope (calculated as the relative change in the number of mature plants over time in comparison to pre-fire population size) for multiple fires under current (baseline scenario, blue) and future conditions (RCP4.5, orange and RCP8.5, red) for a fire interval of 13 years. Lines show median values of 30 repetitions and shaded areas the upper and lower quartiles. Horizontal line indicates the threshold for self-replacement.

3. Results

For the current mean fire interval of 13 years, estimated populations are viable and stable under the baseline scenario and the moderate RCP4.5 scenario (Fig. 2, for underlying dynamics of seeds, seedlings and mature plants see Appendix C, Fig. C1). For the RCP8.5 scenario, the high probability of dry years leads to rapid extinction of the population. In the following, we present the results of the four consecutive simulation experiments to evaluate the Interval Squeeze Model.

3.1. Demographic shift

Irrespective of climatic conditions (current climate, RCP4.5 and RCP8.5), the number of seeds reaches a peak at around 20 years after fire and declines thereafter (Fig. 3a). By plant age 35 years the stand level seed store has markedly declined as seeds are lost from old cones and senescing plants. Climate change impacts the absolute number of seeds: their numbers are highest for current conditions and decrease with drier conditions. Additionally, the onset of seed production is later for the RCP8.5 scenario.

3.1.1. Post-fire-recruitment shift

The recruitment probability was calculated as the number of recruited seedlings four years after fire in relation to the total number of seeds released at the time of fire. The recruitment probability decreases with increasing probability of dry years, leading to a significant decline of the median under severe climate change (Fig. 3b, see Appendix B for p and W values of the Wilcoxon rank sum test). At the same time, variability in recruitment probability also decreases between RCP4.5 and RCP8.5.

3.1.2. Demographic envelope

For the baseline scenario (Fig. 3c), the time interval of successful self-replacement ranges from five to thirteen years. If the next fire event occurred within this time range, the number of mature plants at the time of fire occurrence would be higher than the number at the previous fire. However, this does not reflect, that seed production might not have started, yet (Fig. 3a), potentially leading to an extinction of the population after the next fire. For the RCP4.5 and RCP8.5, the median values indicate that self-replacement does not occur after the first fire, but since there is a high variability between simulation runs, in 25% of the runs self-replacement is possible for the same interval as for the baseline scenario. Simulation runs, in which self-replacement was tested after a second fire instead after the first, showed an increased probability of self-replacement for the RCP4.5 scenario.

3.1.3. Interval squeeze

To assess the combined impacts of drier conditions and a change in the mean fire interval on population viability, we evaluated how long it took, within a total simulation time of 200 years, before self-replacement was no longer possible for different fixed fire intervals with multiple fires. A value of 200 years indicates successful self-replacement through to the end of the simulation time, i.e. potentially long-term population viability. For the baseline scenario, long term survival is possible for fire intervals between 10 and 28 years. In the RCP4.5 scenario, the fire interval that allows for population persistence is squeezed to a fire interval of 13–28 years. In the RCP8.5 scenario, all populations go extinct in less than 200 years irrespective of the fire interval and the uncertainty in the survival duration of a population is larger than for the other scenarios. For this scenario, the longest survival durations are reached at intervals between 15 and 23 years.

3.2. Impact of climate change on seeds, seedlings and adults

We assessed the number of seeds, seedlings and adult plants for different climate conditions to determine the contribution of changes in different demographic processes to overall population performance under drier conditions. Table 3 shows results from simulations of a single fire event occurring in year 8. We determined the number of seeds in the year before the fire, the number of seedlings four years after the fire, and the number of adults 13 years after the fire. The absolute and relative loss of individuals between demographic stages is largest from the seed to the seedling stage, with survival rates lower than 1%. Losses are higher for the RCP4.5 and RCP8.5 scenarios than for the baseline scenario. The overall losses are smaller from the seedling to the adult stage. During the demographic process of establishment (i.e. growth from seedling to mature plant), up to about half of the individuals can survive and establish. All in all, the total number of seeds versus adult plants differs by two to three orders of magnitude.

Comparing the climate scenarios shows that the total number of individuals decreases with increasing dry year probability. To assess the impact of higher dry year probabilities on the three demographic processes we transformed the results relative to the medians of the respective demographic stage in the baseline scenario (Fig. 4). For all demographic stages, the relative reduction is much higher for RCP8.5 than for RCP4.5. For RCP4.5, the highest reduction compared to the baseline scenario occurs during the seedling stage, and the RCP8.5 scenario shows high reductions during seedling and adult stages compared to the baseline scenario.

4. Discussion

Our results confirm the hypothesis of the Interval Squeeze Model that shorter fire intervals in combination with drying climate are highly likely to cause a decline (and possible extinction) in serotinous non-sprouting MTE shrubland plant species. Our model results also show that future population persistence under drier conditions would require longer fire intervals for the RCP4.5

scenario, and that persistence is not possible for the RCP8.5 scenario. This is in contrast with a pure correlative study using species distribution modelling to assess range contractions of extractions of Banksia species in response to changing climate (Yates et al., 2010). Here, a general increase in the range of *Banksia hookeriana* was found, if land transformations were not accounted for. However, this estimate did not include any demographic processes or impacts of higher fire frequency.

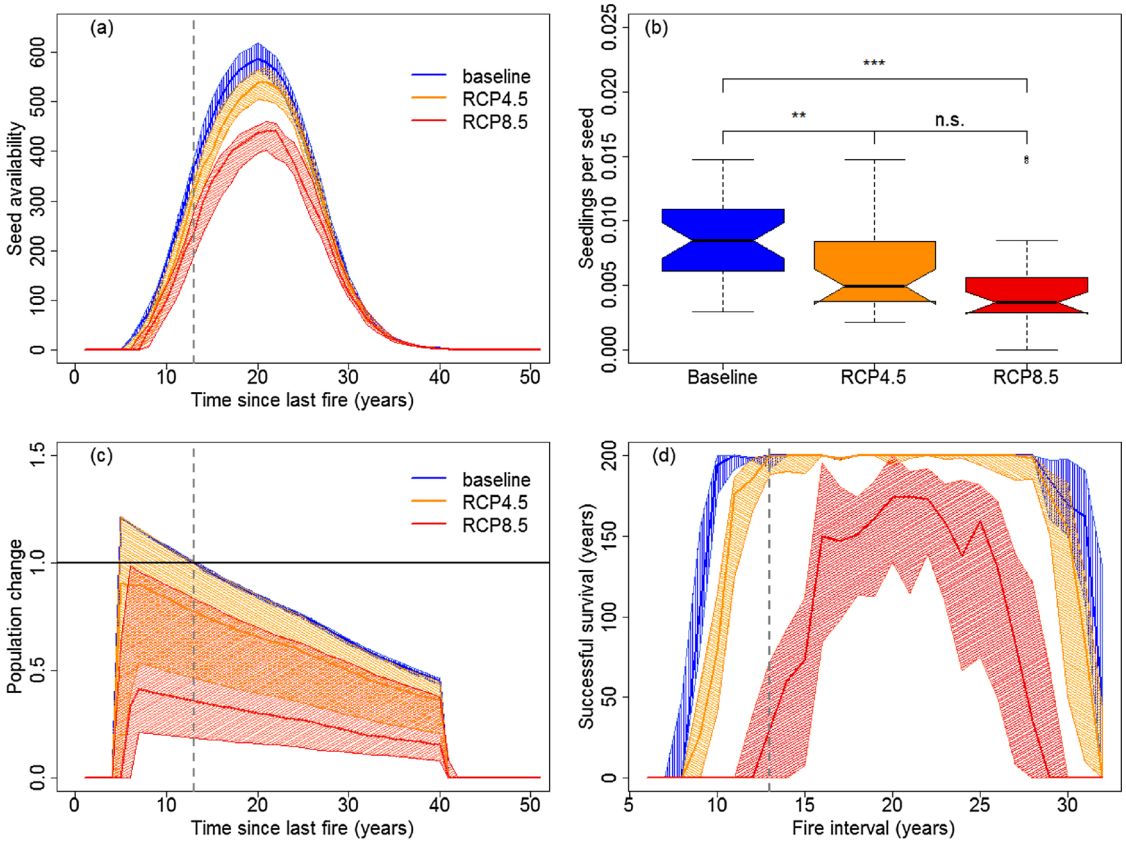

Fig. 3. Simulated components of the Demographic Squeeze Model for Banksia hookeriana under present and future climate conditions. a) Demographic shift shown as seed availability per plant over time in the absence of fire, b) post-fire-recruitment shift of plants given as the fraction of seeds that germinated and survived to the 4th year after fire, c) demographic envelope calculated as the relative change in the number of mature shrubs over time in comparison to pre-fire population size, and d) Interval Squeeze as the viable fire interval time window (i.e. of successful self-replacement) for fixed fire intervals ranging from 6 to 32 years. The lines in a), c) and d) show median values and shaded areas the lower and upper quartiles. The dashed grey line indicates the current estimated mean fire interval of 13 years, and the black horizontal line in c) indicates the threshold for self-replacement. Boxes in b) show the median as well as upper and lower quartiles with significant differences between climate scenarios indicated by asterisks (n.s.: not significant $p \geq 0.05$, **: $p < 0.01$, ***: $p < 0.001$). Simulations for each scenario were replicated 30 times.

Table 3
Median and quartiles of the number of seeds (year before the fire), seedlings (year four, i.e. before reaching maturity), adults (year 13, before fire) and percentage of individuals that reach the subsequent demographic stage after fire.

	Baseline Median (lower / upper quartile)	RCP4.5 Median (lower / upper quartile)	RCP8.5 Median (lower / upper quartile)
Seeds before fire	$6.77\ 10^5$ ($6.24\ 10^5$ – 7.1210^5)	$5.72\ 10^5$ ($5.13\ 10^5$–$6.11\ 10^5$)	$4.89\ 10^5$ ($4.16\ 10^5$–$5.31\ 10^5$)
Seedlings	$5.83\ 10^3$ ($3.40\ 10^3$ – $7.25\ 10^3$)	$2.83\ 10^3$ ($1.85\ 10^3$ – $4.47\ 10^3$)	$1.67\ 10^3$ ($0.98\ 10^3$ – $2.63\ 10^3$)
Seedlings as % of seeds	0.86	0.50	0.34
Adult plants	$2.01\ 10^3$ ($1.99\ 10^3$ – $2.03\ 10^3$)	$1.55\ 10^3$ ($0.93\ 10^3$ – $2.01\ 10^3$)	$0.71\ 10^3$ ($0.38\ 10^3$ – 1.6710^3)
Adults as % of seedlings	34.5	54.7	42.8

4.1. The role of demographic processes under drier conditions

During post-fire stand development, fire-killed plant populations undergo consecutive steps, during which the potential population size of the next generation can be drastically decreased. In our simulation experiment, these steps are clearly separable, since the population forms an even-aged cohort: as a result of fire all plants of the old generation are killed, and a new generation establishes from seeds germinating in the first year after a fire. In our experiments, we assumed plant traits and experienced environmental settings to be the same for each individual. Since we are simulating cohorts in a spatially implicit landscape, accounting for individual differences would not have altered the general outcome, but would have increased the variance of results.

The first demographic process that we evaluated was seed production. Based on empirical findings (Keith et al., 2014), we assumed a lower number of newly produced seeds per plant in years with below average rainfall conditions, and a later onset of reproduction. This led to a lower total number of seeds per plant in our two climate change scenario simulations relative to the baseline. The peak in seed availability was reached for all climate scenarios when the number of newly produced seeds equaled the number of seeds that had reached their

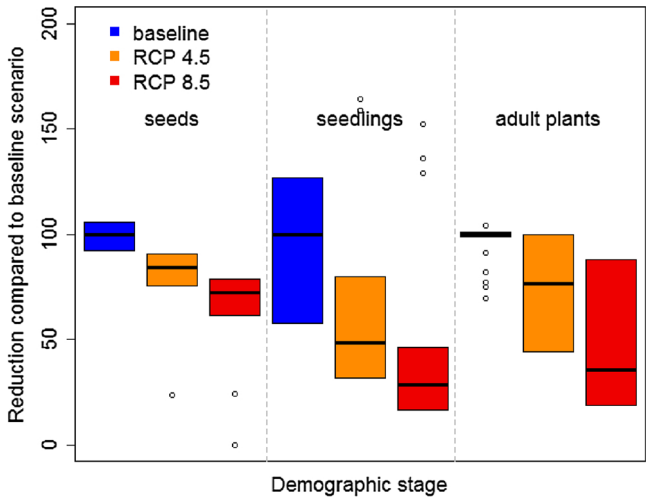

Fig. 4. Relative contribution of each demographic stage (seed availability, survival of seedlings, survival of adult plants) to the total decline in population size under drier conditions. For comparability, all data were transposed relative to the median of the respective demographic stage under baseline conditions. The point of time for the evaluation was the year before fire for seeds, year four for seedlings and year 13 for adults. Boxes show the median as well as upper and lower quartiles. Simulations for each scenario were replicated 30 times.

maximum longevity of 15 years. Afterwards the number of available seeds declined strongly, not only for a single plant, but also for the whole population, since it consists of an even-aged, senescing cohort. The next demographic stage, seedlings, is adversely affected by drier conditions because seedling mortality is higher under dry than under average conditions (Enright et al., 2014). This higher seedling mortality led to a lower ratio of seedlings per seed under the increasingly dry and very dry conditions of the RCP4.5 and RCP8.5 scenarios than for the baseline scenario (Post-fire recruitment shift, Fig. 3b): While the median survival rate of seedlings after four years was 0.85% for the baseline scenario, this decreased to 0.49% for RCP4.5 and to 0.37% for RCP8.5. The largest difference between results for historic climate conditions and results for the RCP8.5 scenario is found for the demographic envelope, which describes the population change in terms of adult plants over time compared to pre-fire population size. The envelope after a single fire event shows a higher variability for the RCP4.5 scenario compared to the baseline scenario, and successful self-replacement only occurred in less than half of the replicates. No successful self-replacement is possible for the RCP8.5 scenario. Therefore, the population will not survive under climatic conditions of the RCP8.5 scenario, as also apparent for the overall Interval Squeeze accounting for multiple fires (Fig. 3d). But also under the RCP4.5 scenario, survival would be threatened, if additionally the fire interval was shorter than today. Our analyses show the results of a fixed, non-random fire interval, which certainly affects the range of the fire interval allowing for population survival: For short mean fire intervals, which allow for survival under the assumption of a fixed fire interval, the probability of extinction would increase. This is caused by the high probability of occurrence of occasional very short inter-fire periods, which would not allow enough time for accumulation of a sufficient seed store. Due to the non-linear response of the population, this negative impact cannot be balanced by positive impacts of longer inter-fire periods. The same applies for long mean fire intervals, for which under random occurrence of fire, seed longevity could be exceeded for some very long inter-fire period, again leading to extinction of the population. Thus, accounting for random processes in the fire interval would overall decrease the range of the mean fire interval compatible with population persistence.

When comparing the absolute numbers of seeds, seedlings and adults, it becomes evident that generally, the germination of seeds and the survival of seedlings is the biggest bottleneck in the survival of this species, which is also evident from empirical studies (Enright et al., 2014): Even under current climate conditions, less than 1% of seeds are still alive as seedlings after four years. The bottleneck of maturity is much less pronounced, and more than 30% of the seedlings that were alive in year four are still alive as mature plants after nine additional years. Plants have adapted to these bottlenecks by producing a very high number of seeds (up to 1400 per plant (Enright et al., 1996) to compensate for these high losses. In the climate change scenarios, populations have a slightly reduced total seed number under the RCP4.5 (84% of the baseline scenario) and a stronger reduced number under the RCP8.5 scenario (72%). This is caused by two factors: the total plant number directly before the first fire event occurs is lower due to increased plant mortality, and each plant produces less seeds as a result of dryer conditions. That is, while the survival of seedlings is the major survival bottleneck under present climate, the number of available seeds will become an additional bottleneck under future conditions, especially for conditions as predicted for the RCP8.5 scenario. These differences in seed availabilities are then accentuated in the next demographic steps.

In our study, we focused on drier climate conditions in combination with more frequent fires to quantitatively evaluate the Interval Squeeze Model proposed by Enright et al. (2015). However, especially in woodlands, increased aridity can lower productivity and thus the availability of fuel. Therefore, in woodlands, fire activity may also decrease in response to climate change (Bradstock, 2010). In case of moderate changes in climate as assumed in the RCP4.5 scenario, *B. hookeriana* might still persist in the future under less frequent fires, as shown in the Interval Squeeze simulations (Fig. 3d). However, in case of strong changes in climate (RCP8.5), the combination of lower seed production with higher seedling and adult mortality will lead to extinction of this species regardless of the fire interval.

4.2. Buffer mechanisms under altered conditions

Our results suggest that more frequent dry years and shorter fire intervals generate synergistic effects, which reduce population persistence of *B. hookeriana* as compared to either driver alone. This synergistic effect has also been found in a landscape model of MTEs, which explicitly highlighted the combined impacts of fire and soil moisture on vegetation succession (Millington et al., 2009). In our case, the combination of both stressors negatively affects seed availability as a starting point for the next generation. In this regard, the seedbank can be seen as a buffer mechanism of the population against fires. Buffer mechanisms often play an important role for the dynamics of ecosystem variables (Jeltsch et al., 2000). In our case, the buffer mechanism is reduced as a result of drier conditions and because more frequent fire intervals do not allow sufficient time for seed accumulation, therefore, the population viability decreases.

Kelly and Brotons (2017) suggested using life history traits to estimate upper and lower bounds of fire intervals and to use these to avoid species extinctions and thus to promote biodiversity. Our simple, spatially implicit model allowed us to quantify these bounds for *B. hookeriana*. Alternatively, we could use the model in a follow-up approach to systematically assess the impact of life history traits on shifts of these bounds. Here, we could test how the finding might differ for plants with different traits related to dispersal and recruitment, e.g. plants with a lesser degree of serotiny or with a soil seedbank.

In a field study covering four post-fire years at 33 sites with different interfire intervals Enright et al. (2014) showed that species with a soil seedbank and species with the ability to resprout were less vulnerable to shortened fire intervals. A proportion of seeds from species with a soil seedbank do not germinate after a fire (Auld and Denham, 2006) which may constitute a buffer mechanism against adverse recruitment conditions in post-fire years. Resprouting species have the advantage that they do not exclusively rely on successful seedling recruitment for population persistence. However, the capacity of this buffer mechanism

is limited as well, because very short fire intervals can increase mortality rates in resprouters (Enright et al., 2011). In addition, when mature plants cannot be replaced due to low recruitment, long-term adverse effects due to ageing of the population are likely (Enright et al., 2014).

Additional buffer mechanisms may work at other ecological levels than at the level of the individual plant or of the population. For example, Batllori et al. (2017) suggested in their modelling study that vegetation heterogeneity in the landscape might mediate synergistic effects of changing fire frequencies and drought on MTE vegetation. Also, vegetation diversity can constitute a buffer mechanism that has been shown to mitigate the loss of ecosystem functionality through climate change in drylands, including MTEs (Maestre et al., 2012). Thus, trait-based demographic approaches are needed to increase our understanding of how future plant communities may be structured and whether ecosystems will be able to retain their functioning.

5. Conclusion

Using a simple vegetation model, which we parameterized for a population of the serotinous, fire-killed shrub, *Banksia hookeriana*, we found that a drying climate reduces the range of fire intervals compatible with population persistence. While the required fire interval for persistence is longer under future, drier climate, actual fire intervals are projected to become shorter, leading to a strong mismatch. This mismatching effect of multiple stressors poses a threat for *B. hookeriana*, but might differ for species with different traits, such as resprouters and inter-fire recruiters. This presents a challenge for managers who must find ways to reconcile biodiversity conservation needs and fire hazard reduction objectives.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ecolmodel.2018.10.010.

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